

Biological soil crusts in grazed and ungrazed Wyoming sagebrush steppe

J.M. Muscha*, A.L. Hild

Department of Renewable Resources, University of Wyoming, Laramie, WY 82070, USA

Received 9 August 2004; received in revised form 5 December 2005; accepted 22 February 2006

Available online 3 April 2006

Abstract

Biological soil crusts are regarded as an indicator of healthy landscapes. To understand the response of biological soil crusts to grazing in northern sagebrush steppe, we examined nine *Artemisia*-dominated sites in Wyoming where livestock have been excluded for 32–45 years. Using two common sampling methods (20 m line transects and 0.25 m² quadrats) we determined biological soil crust cover and richness inside and outside exclosures. Total biological soil crust cover did not differ inside and outside the exclosures at any of the nine sites, regardless of monitoring method. Cover of biological soil crusts using the transect method ranged from 2% to 8% inside and 1% to 6% outside the exclosure. Cover of biological soil crusts using the quadrat method ranged from 2% to 11% inside and 2% to 9% outside the exclosure. Fruticose lichen cover was greater outside the exclosure at two sites (Poison Spider and Lander Ant) using the quadrat method. Both methods show a decrease in moss outside exclosures when assessed across all sites. Lichen and moss richness ranged from 5 to 15 species at each site. Fourteen of the 34 species collected throughout the sites were found only at one of the nine sites, and they did not all occur together or at the same site. Our results suggest that 32–45 years of grazing removal has not increased soil lichen cover but did increase moss cover inside exclosures. Distinguishing biological soil crusts by morphological groups aided recognition of differences that would not be apparent in an analysis by species.

© 2006 Elsevier Ltd. All rights reserved.

Keywords: Lichen; Moss; Quadrat; Rangeland exclosures; Sandy loam soils; Transect

*Corresponding author. USDA-ARS Fort Keogh Livestock and Range Research Laboratory, 243 Fort Keogh Road, Miles City, MT, 59301, USA. Tel.: +406 232 8223; fax: +406 232 8209.

E-mail addresses: jennifer@larrl.ars.usda.gov (J.M. Muscha), annhild@uwyo.edu (A.L. Hild).

1. Introduction

The ecological importance of biological soil crust cover has become apparent in the past two decades. Biological soil crusts inhabit open spaces among vascular plants and beneath canopy spaces in arid and semi-arid grassland and shrubland ecosystems. They improve soil fertility in typically nutrient-poor systems (Belnap and Gardner, 1993; Beymer and Klopatek, 1991; Evans and Ehleringer, 1993) and reduce erosion by binding soil particles (Eldridge, 1998). In arid systems, biological soil crusts can enhance establishment of vascular plants by altering soil temperatures and improving soil water retention (DeFalco et al., 2001).

The detrimental effects of grazing livestock on biological soil crusts have been documented in the Great Basin (Jeffries and Klopatek, 1987; Kleiner and Harper, 1977; Marble and Harper, 1989), desert south-west (Beymer and Klopatek, 1992; Brotherson et al., 1983), and cool deserts of east central (Kaltenecker et al., 1999) and south central (Memmott et al., 1998) Idaho. Recovery of crusts following disturbance depends on the severity of disturbance and the subsequent climatic and vegetative conditions but are estimated to take from 5 to 250 years (Anderson et al., 1982b; Belnap, 1993; Callison et al., 1985; Cole, 1990; Jeffries and Klopatek, 1987). Most North American work on biological soil crusts has been conducted in the Desert South West and Great Basin where cover of vascular plants is low. Generally, total crust cover is inversely related to vascular plant cover, as less plant cover leaves more soil surfaces available for crust colonization, and is positively correlated with increased precipitation (Rosentreter and Belnap, 2001). Little is known, however, about the dynamics of biological soil crusts in northern sagebrush steppe systems which differ from the Great Basin and Desert South West in its denser stands of *Artemisia*, and greater cover of perennial grasses within shrub interspaces (West, 1988). Response of biological soil crusts to livestock trampling and their recovery rates may differ in northern sagebrush steppe systems.

Earlier studies have found significant links between the cover and diversity of soil crusts, and some indices of landscape health. In general, healthy, stable landscapes dominated by native vegetation contain higher diversity and cover of biotic crusts (Eldridge and Koen, 1998; Rosentreter and Eldridge, 2002). The objective of our study was to document the richness and cover of biological soil crusts at nine rangeland sites in the northern sagebrush steppe of Wyoming, USA, after 32–45 years of livestock exclusion. We compared two common sampling methods for determining biological soil crust cover within and outside of exclosures at the nine sites to document the effects of grazing removal on lichen and moss cover.

2. Methods

The nine exclosure sites were within sagebrush steppe in Natrona, Fremont, Sweetwater, Hot Springs and Washakie counties in Wyoming (Fig. 1). Exclosure age ranged from 32 to 45 years (Fig. 1) and size ranged from 2.5 to 12.5 ha. The topography was relatively flat to gently sloping, slopes ranged from 0% to 8%. Bison were historically distributed throughout the sagebrush steppe, but most abundant in south-western Wyoming and south-eastern Idaho (Van Vuren, 1987; Urness, 1989) and on the shortgrass plains in eastern Wyoming (Dorn, 1986). Dominant grass species found at exclosure sites were *Agropyron smithii* Rydb., *Poa secunda* J.Presl, *Agropyron spicatum* (Pursh) Scribn. &

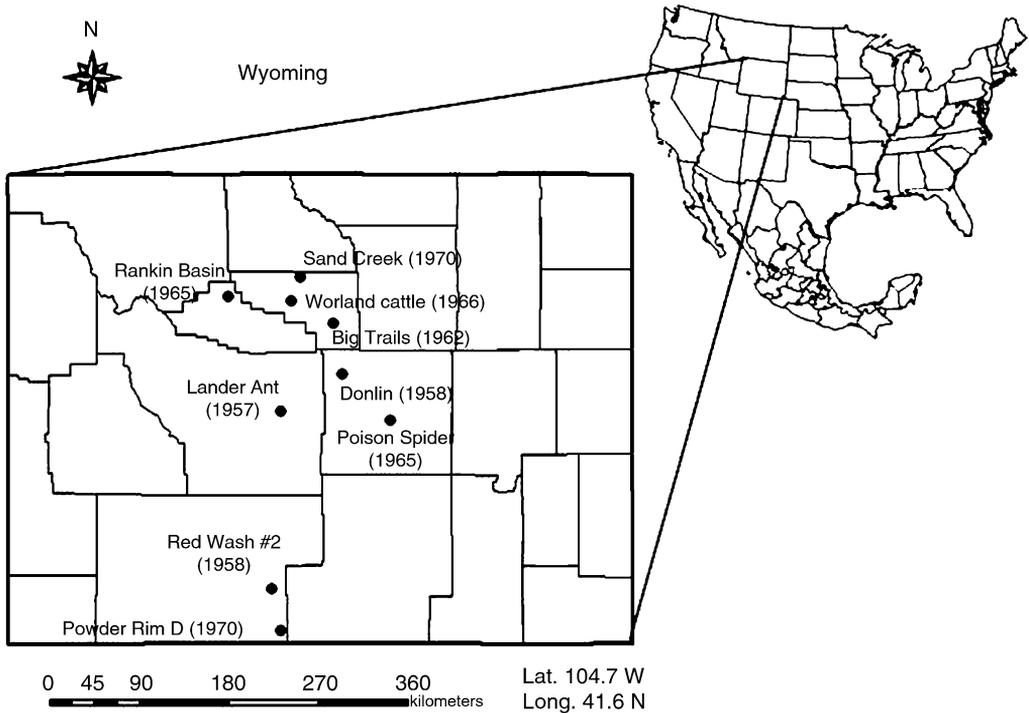


Fig. 1. Location and establishment year of nine range enclosures sampled in Wyoming in 2001 and 2002.

J.G.Sm., *Stipa comata* Trin. & Rupr., *Koeleria macrantha* (Ledeb.) Schult., and *Bouteloua gracilis* (Kunth) Lag. ex Griffiths. Donlin was the only enclosure dominated by *Carex filifolia* Nutt. *Bromus tectorum* L., an exotic annual grass, was present at five of the nine sites (Poison Spider, Big Trails, Powder Rim D, Worland Cattle, and Sand Creek). Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) was the dominant shrub at each site (Table 1). Poison Spider was the only site where shrub cover was greater inside (40%) than outside (22%) the enclosure (Muscha et al., 2004). The enclosure sites represent a variety of elevation, precipitation and soil characteristics (Table 1). Soils at the study sites are coarse-loamy and fine-loamy mixed, mesic families of Typic Haplocalcids and Calcargids. We determined soil surface texture by analyzing soil samples retrieved from inside and outside the enclosures (Gee and Bauder, 1986). Seven enclosures in our study have sandy loam soil textures; two sites (Rankin Basin and Red Wash #2) have sandy clay loam soil textures. Grazing history at each enclosure site was obtained from records maintained at the Bureau of Land Management district offices in Wyoming.

Two methods were used to sample cover of biological soil crusts. In June and July 2001 and 2002 we placed four vegetation line transects (20 m) in each of two positions (inside and outside) at each large enclosure (Big Trails, Poison Spider, Lander Ant, Sand Creek, Red Wash #2), and three transects were placed in each position (inside and outside) at each small enclosure (Donlin, Powder Rim D, Rankin Basin, Worland Cattle), resulting in a

Table 1
Site characteristics of nine Wyoming shrubland exclosures sampled in 2001 and 2002

Exclosure name	Established (year)	Elevation (m)	Annual precipitation (mm)	Dominant grass and sedge (in order of abundance)	Native ^a grass (%)	Shrub ^a (%)	Bare ^b ground (%)	Sand (%)	Silt (%)	Clay (%)
Big trails	1962	1515	348	<i>Agropyron smithii</i> , <i>Agropyron spicatum</i> , <i>Bromus tectorum</i>						
In					27	21	20	66	16	18
Out					21	16	52	59	21	20
Poison Spider	1965	1758	303	<i>Bromus tectorum</i> , <i>Poa secunda</i> , <i>Agropyron smithii</i> , <i>Koeleria macrantha</i>						
In					12	40	22	59	21	20
Out					23	22	49	47	28	25
Donlin	1958	1879	285	<i>Carex filifolia</i> , <i>Stipa comata</i>						
In					39	11	62	61	29	10
Out					44	8	81	62	29	9
Powder rim D	1970	1939	277	<i>Stipa comata</i> , <i>Poa secunda</i>						
In					36	6	68	75	12	13
Out					11	6	84	81	7	12
Lander ant	1957	1621	221	<i>Stipa comata</i> , <i>Bouteloua gracilis</i> , <i>Poa secunda</i> , <i>Agropyron smithii</i>						
In					32	22	61	66	17	17
Out					31	16	64	65	18	17
Worland cattle	1970	1300	194	<i>Stipa comata</i> , <i>Bromus tectorum</i> , <i>Agropyron smithii</i>						
In					11	21	65	75	17	8
Out					7	18	59	71	20	9
Sand creek	1966	1333	194	<i>Stipa comata</i> , <i>Poa secunda</i>						
In					9	13	66	83	1	16
Out					3	11	68	64	18	18
Rankin basin	1958	1932	172	<i>Bouteloua gracilis</i> , <i>Stipa comata</i>						
In					5	17	45	50	26	24
Out					11	17	56	49	25	26
Red wash #2	1965	1576	258	<i>Stipa comata</i> , <i>Oryzopsis hymenoides</i> , <i>Agropyron spicatum</i>						
In					14	15	77	56	22	22
Out					38	18	78	56	23	21

^aPercent cover recorded from canopy cover transect.

^bPercent bare ground recorded from basal cover transect.

total of 64 transects. Intercepted basal cover of biological soil crusts was recorded along the line transects.

In the first summer (2001), we recorded very little biological soil crust cover using the transect method at the first five sites sampled. To more intensively sample the sites, we added a quadrat technique to the study in 2002. Ten permanent quadrats (20 × 50 cm) were randomly placed between transects at each position inside and outside of the exclosures at each site. At each randomly selected location, a sampling quadrat was centered over the nearest crust (lichen or moss) and then oriented so that its longest side was parallel to the line transects. Quadrats were placed at least 5 m away from each transect, and each quadrat location was permanently marked with a numbered aluminum tag. Percent cover of each soil crust was recorded within each quadrat, using ocular estimates. The area within each quadrat was wetted with a hand held spray bottle (Rosentreter and Eldridge, 2002) prior to sampling to improve visibility and identification of biological soil crusts. In addition, we surveyed the exclosure site for crust species not present within the quadrats. A representative sample of each moss and lichen species was collected outside the quadrats and archivally mounted for preservation. Mounted species were used to verify field identification and are retained in the Shrubland Ecology Laboratory at the University of Wyoming. All quadrat sampling was conducted in May and June of 2002. Crust cover values were recorded for three morphological groups: mosses, fruticose soil lichen species, and all other soil lichens (Eldridge and Rosentreter, 1999). Species richness of mosses and lichens at each site was based on voucher specimens and represents site richness rather than only species encountered in quadrats.

2.1. Experimental design and data analysis

It is unfortunate that most exclosure and relict sites (in Wyoming and elsewhere) do not have replicated exclosure treatments. Ideally, it would have been statistically advantageous to have constructed three or more exclosures at each site. The lack of replicated exclosures within a site is a common problem in exclosure, wildfire, and relict research where remnant vegetation has been preserved (for example Pettit et al., 1995; Hargrave and Seastedt, 1994; Hester and Hobbs, 1992; Quinn and Walgenbach, 1990 and many others). Because we were not present more than 50 years ago, when the fencing was established, we are forced to treat randomly located quadrats or transects within and outside of exclosures as replicates of the two positions relative to the fence. The consequences of this approach are that replicates may be less variable than they might have been if placed in three or four separate exclosures on the site, and consequently we may declare *more* differences between site or position treatments than might occur under ideal design conditions. We also must treat both site and position treatments as fixed effects. Position treatments are either “in” or “out” by virtue of the fence position. Additionally, the particular exclosure sites were not randomly selected but were chosen based upon fence integrity, distribution in the state, elevation and presence of Wyoming big sagebrush. Each site has a unique history and we cannot insure that the selected sites are a random sample of all Wyoming big sagebrush steppe vegetation. It is not possible to discern from historic records how the exclosure sites were selected initially. Extrapolation of our results beyond the unique constraints of our particular study sites should be approached with caution.

Total biological soil crust cover from transect and quadrat data was assessed with analysis of variance (ANOVA) as a series of experiments following Cochran and Cox

(1957, chapter 14) using site and position in a factorial combination. Treatment effects are tested against a pooled error term using each quadrat or transect as replicates. This analysis assumes fixed treatment effects. This approach allows for comparison of positions, sites, and their interaction. We analyzed each of the morphological groups of biological soil crusts (moss, fruticose lichen, and other lichen) in the same manner to determine if morphological groups reveal more discerning position differences not apparent from total crust cover. Where *F*-tests were significant ($\alpha = 0.05$), we used Fisher's protected least significant differences (FLSD) to conduct mean separation.

3. Results

In general, cover of moss, fruticose lichens, and other lichen crust differed among the nine sites, regardless of the sampling method used (Table 2). Total crust cover also differed among sites using the quadrat method, but not in the transect data. Overall, both methods reveal site and position differences, but only the quadrat method discerned an interaction of site and position in fruticose lichen cover. As reported in Muscha et al. (2004), the vascular plant community differed between positions only in a few exclosures. At Powder Rim D, native grass cover was greater inside the exclosure and at two sites (Red Wash #2 and Poison Spider) native grass cover was greater outside the exclosure. *B. tectorum* cover was greater inside Poison Spider and Big Trails exclosures. Big Trails, Poison Spider, and Donlin had more bare soil and less litter cover outside than inside exclosures. Soil crust cover on the nine exclosure sites, is roughly ordered from most mesic (Big Trails and Poison Spider) to most xeric (Red Wash #2) based on annual precipitation and soil texture differences (Figs. 2 and 3).

3.1. Crust cover on transects

Total biological soil crust cover (all morphological groups together) did not differ among sites or between positions when averaged across sites (Fig. 2). When averaged across sites, moss cover was greater inside (3.0%) than outside (1.6%) exclosures. Fruticose lichen cover was absent from four of the exclosure sites (Red Wash #2, Sand

Table 2

F-test probability values for (a) transect data and (b) quadrat data analysis of variance (ANOVA) results for four biological soil crust attributes at nine exclosures in Wyoming

Source	DF	Total crust	Moss	Fruticose Lichen	Other Lichen
(a) <i>Transect data</i>					
Site	8	.0517	.0102	<.0001	<.0001
Position	1	.1537	.0302	.0595	.1897
Site*Position	8	.4273	.5300	.3337	.1770
Error <i>b</i>	46	—	—	—	—
(b) <i>Quadrat data</i>					
Site	8	<.0001	.0039	<.0001	<.0001
Position	1	.1120	.0191	.0084	.3945
Site*Position	8	.9427	.7101	.0138	.9287
Error <i>b</i>	130	—	—	—	—

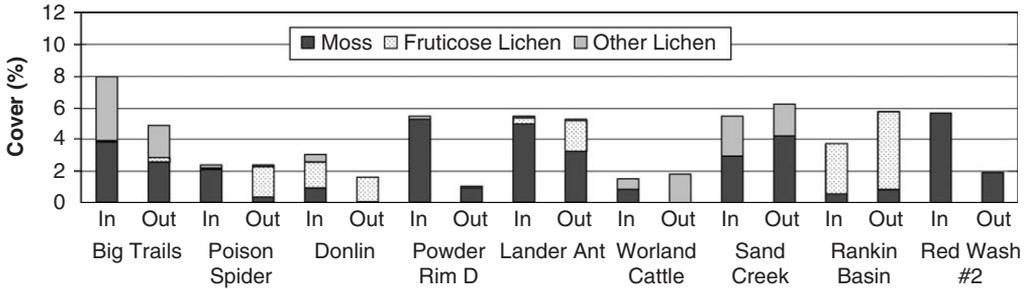


Fig. 2. Transect documentation of biological soil crust cover (moss, fruticose lichen, other lichen) in two positions (inside and outside grazing exclosures) at nine sagebrush study sites in Wyoming. Means are based on cover from 3 to 4 20 m line transects within each position and site, monitored over the 2001 and 2002 growing seasons. Exclosure locations are arranged roughly from most mesic (Big Trails) to most xeric (Red Wash #2).

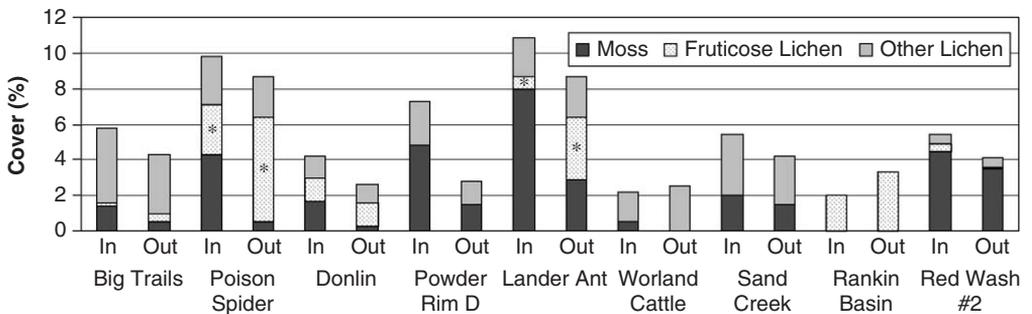


Fig. 3. Quadrat documentation of biological soil crust cover (moss, fruticose lichen, other lichen) in two positions (inside and outside exclosures) at nine sagebrush study sites in Wyoming. Within a site and cover type; asterisks delineate significant differences between inside and outside positions; $p < 0.05$. Means of each crust cover are based on ten 0.1 m² quadrats sampled in 2001 and 2002 field seasons. Sites are arranged roughly from most mesic (Big Trails) to most xeric (Red Wash #2).

Creek, Worland Cattle and Powder Rim D) and when averaged across sites, was not different between positions. Other lichen cover differed among sites regardless of position (no site*position interaction), and cover was greater at Big Trails and Sand Creek (Fig. 2) than at the other sites.

3.2. Crust cover within quadrats

These cover estimates for total crust, moss, and other lichen paralleled results from transect samples (Table 2a and b). Total crust cover was greater at Poison Spider and Lander Ant than at other sites (Fig. 3). Fruticose lichens were absent from three sites (Sand Creek, Worland Cattle and Powder Rim D). Fruticose lichen cover was greater outside than inside exclosures at only the Poison Spider and Lander Ant sites (Fig. 3). When averaged across all sites, moss cover was greater inside the exclosures (3.0%) than outside (1.2%). In contrast, fruticose lichen cover was higher outside (1.6%) than inside (0.8%)

when averaged across sites. Regardless of position (no site*position interaction), other lichen cover was greatest at Big Trails, Sand Creek, and Poison Spider.

3.3. Comparison of the two methods

Both methods were reliable for determining differences among sites in cover of each morphological type of crust, although transects did not detect differences in total crust cover among the sites. The two methods differ in the characterization of fruticose lichens; the quadrat method documented fruticose lichens at the Red Wash #2 site, which was not documented using transects. Because quadrats were centered on crust cover, it seems reasonable that the quadrat method would document more crust species at a given site. In addition, because the fruticose lichen species we encountered are vagrant and irregular shaped, they may be more difficult to discern on transects. The differences in total cover recorded with the two methods (cover >8% in quadrat samples and <8% at all sites from transects) may also be attributed to centering each quadrat on a crust. Transects probably provide a more equitable representation of the absolute abundance of biological soil crust and vegetative cover on a site because this technique did not insure that a crust was sampled. The quadrat method probably provided greater estimates of total crust cover.

3.4. Species richness

Species richness did not differ inside and outside exclosures at all of the nine sites. Rankin Basin and Red Wash #2 (the driest sites in this study) had the fewest crust species present (Table 3). Species richness was greatest at the Poison Spider site (16 species, Table 3). The moss *Tortula ruralis* was the only species found at all nine sites. *Collema tenax* and *Aspicilla* sp. were the most common lichens. All sites had at least five species present, and species richness did not appear to decline with reduced moisture availability. Of the 34 species collected throughout the sites, 14 species were encountered only once.

4. Discussion and conclusions

The similarity in total biological soil crust cover between positions (inside and outside exclosure) and the low cover (<12%) detected by both monitoring methods, may be attributed to a combination of factors. Moss and lichen cover was more abundant beneath shrub canopies than within interspaces, but shrub canopy cover was similar inside and outside positions at 8 sites. Poison spider was the only site where shrub canopy cover was significantly higher inside the exclosure than outside. Since the vegetative community had not changed between inside and outside exclosures at all nine sites, we would expect the soil crust community to also be similar.

We found unexpected differences in crust species presence among our nine sites. Of the 34 species identified in this study, 14 species occurred at only one of the nine sites, and few of these 14 species occurred together at the same site. Eight out of the nine sites had at least one species unique to that specific site. Thus, although other vegetation was similar, the biological soil crust species assemblage appears to vary greatly from site to site. This could be due to differences in soil properties, elevation, annual precipitation, and temperature among sites.

Soil properties can influence the cover and diversity of biological soil crusts. Finer textured soils tend to have higher biological soil crust cover than those with coarse textures (Anderson et al., 1982a). Soils at seven of our nine sites were relatively coarse, sandy soil textures (Muscha, 2003). The coarse soil texture could be one of the driving factors contributing to low crust cover at our sites and the lack of differences between inside and outside positions. Bare-ground cover was still high inside the exclosures at most of our sites even 40 years after grazing was removed. In contrast to our findings, research in the Colorado Plateau and Great Basin has shown that cover of soil crusts are capable of reestablishing back to predisturbance levels in less than 40 years (Anderson et al., 1982b; Callison et al., 1985; Cole, 1990; Belnap, 1993), although species richness recovery may take considerably longer.

Season and intensity of grazing can affect the grazing impact on crusts. Heavy grazing from early to late winter in south-western Utah significantly reduced cover and species richness of crusts, where as grazing only in early winter had little effect (Marble and Harper, 1989). Since soil water is often available in late winter and early spring in that area of the United States, release from grazing in late winter may allow growth of crusts and permit small increases in species richness. Crust cover was higher in control and winter grazed paddocks compared to the spring and summer grazed paddocks in Idaho (Memmott et al., 1998). They concluded that winter grazing with frozen soil conditions appeared to have minimal impact on crusts. It has also been suggested that crusts are more susceptible to disturbance when dry (Anderson et al., 1982a). In Wyoming, most precipitation occurs in spring, particularly during May. Season of grazing, stocking rate, and in some cases type of domestic animal (cattle vs. sheep), have varied greatly at our sites since time of exclosure construction. In some cases grazing use has changed considerably even within the past 10 years (Worland Cattle and Sand Creek). Currently, grazing occurs during winter and early spring at Lander Ant, Rankin Basin, and Red Wash #2, and late spring and fall at Donlin, Worland Cattle, and Sand Creek sites. In contrast, Poison Spider is only grazed in the spring. Big Trails is grazed in the winter one year, spring the following year and rested every third year and Powder Rim D is part of a deferred rotational system and grazed at a different time every year. A light to moderate grazing intensity occurs at all of our sites. None of our sites are grazed year round or in the summer months during the hottest, driest time of the year when the crusts are most susceptible to trampling. This lack of grazing at a time when trampling is detrimental to the crusts could also be a major factor promoting similarity in crust cover and species richness inside and outside exclosures.

In areas where soil crusts predominate, there are often strong associations between morphology and function of crust species such that particular morphologies indicate the degree to which organisms can resist or recover from stress (Eldridge and Rosentreter, 1999). The presence and abundance of individual species or morphological groups of species may be better indicators of rangeland health than total crust cover (Eldridge and Koen, 1998; Eldridge and Rosentreter, 1999). Even though total crust cover was not different between positions, we did find greater cover of fruticose lichens outside two exclosures (Poison Spider and Lander Ant) with the quadrat method. The greater fruticose lichen cover present outside exclosures and increased moss cover inside exclosures in our study agree with findings of Maccracken et al. (1983). They found the fruticose lichen, *Xanthoparmelia chlorochroa*, was more prevalent in areas with reduced vascular plant cover in south-eastern Montana (Maccracken et al., 1983). This lichen, and others in the

same genus, occurred at six of our nine sites, and their cover was greater outside than inside the exclosures. In contrast, mosses are more susceptible to grazing disturbance than lichens (Anderson et al., 1982b; Brotherson et al., 1983; West, 1990; Memmott et al., 1998). Because mosses are commonly associated with shrub cover, the increased moss prevalence inside exclosures may be related to increased shrub cover inside exclosures. Future studies should consider this association when documenting mosses. Our findings emphasize the importance of discerning morphological groups when sampling biological soil crusts because total crust cover did not differ between positions using either method, but certain morphological groups were different.

Applications of our results are limited to the unique geologic, climatic, and management history of central Wyoming and extrapolation to other geographic regions is not appropriate. Studies of biological soil crusts in other regions have demonstrated more dramatic response to grazing treatments, likely because of environmental constraints in those regions. For example, Belnap (1993) and others (Belnap and Gardner, 1993; Belnap and Eldridge, 2001) found very slow rates of recovery in crusts of the Colorado Plateau and the Great Basin, where climatic constraints, evolutionary exposure to herbivory, and the entry of invasive species into native communities make those ecosystems much more susceptible to the impacts of herbivory and soil disturbance. Exclosures in Wyoming sagebrush steppe where *Agropyron smithii*, *A. spicatum*, *Stipa comata*, *Poa secunda* and *Koeleria macrantha* are common would be expected to contain fewer crusts and more herbaceous perennials. Our results demonstrate fewer differences in biological soil crust cover attributable to removal of domestic livestock than studies in the Colorado Plateau and Great Basin ecoregions.

Although current grazing management at our nine sites is maintaining (or sustaining) total cover of biological soil crusts, species richness may not be recovered. We do not know the potential cover of crusts at our sites, or how long recovery of cover and richness may take. Little research of this extent has been conducted in the United States relating biological soil crusts species to rangeland sites where herbivores have been absent for extended time periods. Additional research based on individual morphological groups, is needed to document how rangeland managers can apply this tool to evaluations of rangeland health. Our results demonstrate different impacts of grazing removal on the separated growth forms of biological soil crusts and impacts on crust species richness are not uniform.

Acknowledgements

We thank Roger Rosentreter for assistance in verification of the specimens collected and review of the manuscript. This project was funded, in part, through assistance from the University of Wyoming; College of Agriculture; Competitive Grants Program.

References

- Anderson, D.C., Harper, K.T., Holmgren, R.C., 1982a. Factors influencing development of cryptogamic crusts in Utah deserts. *Journal of Range Management* 35, 180–185.
- Anderson, D.C., Harper, K.T., Rushforth, S.R., 1982b. Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. *Journal of Range Management* 35, 355–359.
- Belnap, J., 1993. Recovery rates of cryptobiotic crusts: inoculant use and assessment methods. *Great Basin Naturalist* 53, 89–95.

- Belnap, J., Gardner, J.S., 1993. Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. *Great Basin Naturalist* 53, 40–47.
- Belnap, J., Eldridge, D., 2001. Disturbance and recovery of biological soil crusts. In: Belnap, J., Lang, O. (Eds.), *Biological Soil Crusts: Structure, Function and Management*. Springer, Berlin, Heidelberg, Germany, pp. 363–383.
- Beymer, R.J., Klopatek, J.M., 1991. Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands. *Arid Soil Research and Rehabilitation* 5, 187–198.
- Beymer, J.D., Klopatek, J.M., 1992. Effects of grazing on cryptogamic crusts in pinyon-juniper woodlands in Grand Canyon National Park. *American Midland Naturalist* 127, 139–148.
- Brotherson, J.D., Rushforth, S.R., Johansen, J.R., 1983. Effects of long-term grazing on cryptogam crust cover in Navajo National Monument, Arizona. *Journal of Range Management* 36, 579–581.
- Callison, J., Brotherson, J.D., Bowns, J.E., 1985. The effects of fire on the blackbrush [*Coleogyne ramosissima*] community of southwestern Utah. *Journal of Range Management* 38, 535–538.
- Cochran, W.G., Cox, J.M., 1957. *Experimental Designs*. Wiley, New York.
- Cole, D.N., 1990. Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park. *Great Basin Naturalist* 50, 321–325.
- DeFalco, L.A., Detling, J.K., Tracy, C.R., Warren, S.D., 2001. Physiological variation among native and exotic winter annual plants associated with microbiotic crusts in the Mojave Desert. *Plant and Soil* 234, 1–14.
- Dorn, R.D., 1986. *The Wyoming Landscape, 1805–1878*. Mountain West Publishing, Cheyenne, WY 94p.
- Eldridge, D.J., 1998. Trampling of microphytic crusts on calcareous soils and its impact on erosion under rain impacted flow. *Catena* 33, 221–239.
- Eldridge, D.J., Koen, T.B., 1998. Cover and floristics of microphytic soil crusts in relation to indices of landscape health. *Plant Ecology* 137, 101–114.
- Eldridge, D.J., Rosentreter, R., 1999. Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. *Journal of Arid Environment* 41, 11–25.
- Evans, R.D., Ehleringer, J.R., 1993. A break in the nitrogen cycle in aridlands? Evidence from ¹⁵N of soils. *Oecologia* 94, 314–317.
- Gee, G.W., Bauder, J.W., 1986. Particle size analysis. In: Klute, A. (Ed.), *Methods of Soil Analysis. Part 1. Physical and Mineralogical Methods*. American Society of Agronomy Inc., Madison, WI, pp. 383–409.
- Hargrave, B.S., Seastedt, T.R., 1994. Nitrogen concentrations of senescent foliage in a relict tall-grass prairie. *Prairie Naturalist* 26, 61–65.
- Hester, A.J., Hobbs, R.J., 1992. Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the western Australian wheatbelt. *Journal of Vegetation Science* 3, 101–108.
- Jeffries, D.L., Klopatek, J.M., 1987. Effects of grazing on the vegetation of the blackbrush association. *Journal of Range Management* 40, 390–392.
- Kaltenecker, J.H., Wicklow-Howard, M.C., Rosentreter, R., 1999. Biological soil crusts in three sagebrush communities recovering from a century of livestock trampling. In: McArthur, D.E., Ostler, K.W., Wambolt, C.L. (Eds.), *Proceedings: shrubland ecotones; Proceedings of the RMRS-P-11*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah.
- Kleiner, E.F., Harper, K.T., 1977. Soil properties in relation to cryptogamic groundcover in Canyonlands National Park. *Journal of Range Management* 30, 202–205.
- Maccracken, J.G., Alexander, L.E., Uresk, W., 1983. An important lichen of southeastern Montana Rangelands. *Journal of Range Management* 36, 35–37.
- Marble, J.R., Harper, K.T., 1989. Effect of timing of grazing on soil-surface cryptogamic communities in Great Basin low-shrub desert: a preliminary report. *Great Basin Naturalist* 49, 104–107.
- Memmott, K.L., Anderson, V.J., Monsen, S.B., 1998. Seasonal grazing impacts on cryptogamic crusts in a cold desert ecosystem. *Journal of Range Management* 51, 547–550.
- Muscha, J.M., 2003. Impacts of grazing removal on vegetation, soils, and biological soil crusts in Wyoming sagebrush steppe. M.S. Thesis, University of Wyoming, Laramie, 76p.
- Muscha, J.M., Hild, A.L., Munn, L.C., Stahl, P.D., 2004. Impacts of livestock exclusion from Wyoming big sagebrush communities. In: Hild, A.L., Shaw, N.L., Meyer, S.E., Booth, D.T., McArthur, E.D. (Eds.), *Seed and Soil Dynamics in Shrubland Ecosystems: Proceedings. Proceedings of the RMRS-P-31*. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Ogden, Utah, pp. 176–182.
- Pettit, N.E., Froend, R.H., Ladd, P.G., 1995. Grazing in remnant woodland vegetation: changes in species composition and life form groups. *Journal of Vegetation Science* 6, 121–130.

- Quinn, M.A., Walgenbach, D.D., 1990. Influence of grazing history on the community structure of grasshoppers of a mixed-grass prairie. *Environmental Entomology* 19, 1756–1766.
- Rosentreter, R., Belnap, J., 2001. Biological soil crusts of North America. In: Belnap, J., Lange, O.L. (Eds.), *Biological Soil Crusts: Structure, Function, and Management*. Springer, Berlin, Germany, pp. 31–50.
- Rosentreter, R., Eldridge, D.J., 2002. Monitoring biodiversity and ecosystem function: grasslands, deserts and steppe. In: Nimis, P.L., Scheidegger, C., Wolseley, P.A. (Eds.), *Monitoring with Lichens ñ Monitoring Lichens*. Kluwer Academic Publishers, Netherlands, pp. 223–237.
- Urness, P., 1989. Why did bison fail west of the Rockies? *Utah Science* 50, 175–179.
- Van Vuren, D., 1987. Bison west of the Rocky Mountains: A review of the theories and an explanation. *Northwest Science* 61, 65–69.
- West, N.E., 1988. Intermountain deserts, shrubsteppes, and woodlands. In: Barbour, M.G., Billings, W.D. (Eds.), *North American Terrestrial Vegetation*. Cambridge University Press, New York, NY, pp. 210–230.
- West, N.E., 1990. Structure and function of microphytic soil crusts in Wildland ecosystems of arid and semi-arid regions. *Advances in Ecological Research* 20, 179–223.